South African Journal of Botany 88 (2013) 152–163

Contents lists available at SciVerse ScienceDirect

South African Journal of Botany

journal homepage: www.elsevier.com/locate/sajb

Effect of soil type and climatic conditions on the growth and flowering phenology of three *Oxalis* species in the Western Cape, South Africa

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ARTICLE INFO

Article history:
Received 12 December 2012
Received in revised form 12 July 2013
Accepted 15 July 2013
Available online xxxx

Edited by AR Magee

Keywords:
Climate change
Flowering
Invasive plants
Oxalis species
Phenology
Soil type

ABSTRACT

Generally, invasive plant species have wide environmental tolerance that enables them to exploit various climatic conditions and soil types, allowing them to invade new habitats easily. In the Cape Floristic Region, South Africa, the diversity of flowering plants can in part be ascribed to variation in these habitat characteristics that limit their distribution. Climate change has been predicted to bring warmer and drier conditions to the region, with possible influences on the climatic barriers that influence species distributions. We tested the effects of soil type and climate on the growth and flowering of the non-weedy *Oxalis tomentosa*, and the two weedy species *Oxalis purpurea* and *Oxalis pes-caprae* on an altitudinal gradient. The three species, all native to the region, exhibit a range of tolerances to environmental conditions: the first is habitat specific whereas the others are both well-known indigenous weeds that have wider tolerance. The results showed that *O. purpurea* tolerates a variety of conditions well, whereas *O. pes-caprae* is more restricted by soil type, but would potentially profit from future climatic changes. *O. tomentosa*, when removed from its native habitat, was stressed under all conditions. These results suggest that habitat-restricted species will be threatened if the predicted level of climate change occurs, while invasive weeds will profit. Studying species responses to different environmental conditions is essential in determining future distributions.

1. Introduction

Weeds are plant species that grow in sites where they are not wanted and that normally have detectable environmental effects (Richardson et al., 2000). Given that they usually have wider environmental tolerances, they are often better able to survive under conditions of environmental change (Dukes and Mooney, 1999; Le Maitre et al., 2004; Richardson and van Wilgen, 2004; Thuiller et al., 2007). Traits facilitating invasions of weeds include fast growth, vigorous spatial growth, bigger size, effective reproductive output and longer and/or earlier flowering compared to native species (Pyšek and Richardson, 2007). Phenology has been suggested as a particularly important trait facilitating invasions: different timing of flowering in comparison to native plants may give invasive alien plants competitive profits associated with increased reproductive output (Pyšek and Richardson, 2007; Godoy et al., 2009). Weed invasions are problematic, since they may alter the original composition, structure and ecology of native vegetation through competition or environmental transformation (Di Castri et al., 1990; Vitousek et al., 1996; Richardson and van Wilgen, 2004). This may pose a threat to the original biodiversity in general, and environmentally restricted endemic species in particular (Vitousek et al., 1996; Wilcove et al., 1998).

Rouget et al. (2004) mapped the potential ranges of invaders in South Africa, Lesotho and Swaziland based on climatic envelope models. They found that most invasive species were confined to an area of <10% of the region, but could potentially invade to up to 40% of the region under current climatic conditions, assuming no edaphic or biotic restrictions are inherent. Bradford and Lauenroth (2006) highlighted the importance of climate to species invasion, as they found suitable climatic conditions to be crucial to the invasion of a cool-season annual grass, *Bromus tectorum* L., on the steppe grasslands. The impacts of weather conditions on invasions are dependent on several factors such as original vegetation and habitat type. This complicates predictions of the exact effects of climate on invasiveness. It is thus important to conduct species-specific studies under different climatic conditions to make any meaningful predictions (Bradley et al., 2010; van Kleunen et al., 2010). Invasive plant species have become an important consideration in our predictions of the effect of global change (Vitousek et al., 1996). The disturbance of ecosystems and elevated CO_2-levels predicted through global climate change would be expected to increase the risk of plant invasions (Dukes and Mooney, 1999; Weltzin et al., 2003; Thuiller et al., 2007). Weeds, both native and non-native, may become an even larger problem, because they are able to survive so well under changing conditions.

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http://dx.doi.org/10.1016/j.sajb.2013.07.012

The Cape Floristic Region (CFR), an area of 87,892 km^2 in the southwestern Cape of South Africa (Cowling and Pressey, 2003), is a global biodiversity hotspot that has an extremely high diversity of flowering plants. The high species richness has in part been ascribed to the environmental heterogeneity of the region (Goldblatt and Manning, 2002). Diverse soil types and varying climatic conditions, e.g. rainfall patterns and altitudinal differences in temperature, have been identified as two of the main determinants of species diversity within the CFR (Goldblatt, 1997; Linder, 2003; Proches et al., 2006a). The CFR also displays exceptional levels of endemism, with a species-level endemism of 68.8% (Linder, 2003), while genus- and family-level endemism is so high that it has been listed as one of the 25 global biodiversity hotspots (Myers et al., 2000). Proches et al. (2006a) reported 84% of the 2100 geophytic species in the region to be endemic. *Oxalis* L. (Oxalidaceae) is the seventh largest genus (Goldblatt and Manning, 2002) and by far the largest geophytic lineage (Proches et al., 2006b) in the CFR. Although more than a third of the southern African species are listed as of conservation concern in the Red Data list (Raimondo et al., 2009), a few included species are globally invasive, e.g. *Oxalis pes-caprae* L. (Lambdon, 2006).

Climate change predictions for the Western Cape foretell temperature rises of about 1.5 °C at the coast and 2–3 °C inland by 2050 (Midgley et al., 2005). Simultaneously rainfall is expected to increase in the late summer, especially on the mountains, and to decrease in early and late winter, thus shortening the rainfall season. The predictions are based on downscaling from six large scale global circulation models that assume the continuation of greenhouse gas emissions at moderate levels (Midgley et al., 2005). The biodiversity of the CFR has been recognised as being especially vulnerable to extinctions under future climate scenarios (Malcolm et al., 2006; Midgley and Thuiller, 2011). This is due to influences on the future distribution of plant species and vegetation zones, for example on the Fynbos–Succulent Karoo boundary in the CFR (Lechemere-Oertel and Cowling, 2001; Agenbag, 2006; Mucina and Rutherford, 2006). Individual species-level responses are also expected, especially among winter-flowering plants. This is supported by results from Dreyer et al. (2006) who found reductions in the flowering period of *Oxalis* species under warmer and drier conditions; *Oxalis* require rain and cooler conditions for the onset of flowering. Globally, there is evidence for altered phenology in plants due to changing climatic conditions (Parmesan and Yohe, 2003). It is clear that such changes can have impacts on the ecosystem due to changing interactions of species. In general, shifts are towards spring advancement, but delayed responses have also been reported (Parmesan and Yohe, 2003).

We evaluate how soil type and altitude (with associated climatic conditions) affect the above-ground resource allocation and flowering phenology of three *Oxalis* species. Two of these are known weeds with wide edaphic tolerances capable of global invasion (*Oxalis pes-caprae* L. and *Oxalis purpurea* L.), while the third is a range-restricted, non-weedy shale endemic (*Oxalis tomentosa* L.f). Although both *O. purpurea* and to a lesser extent *O. pes-caprae* are still present in natural populations in pristine, undisturbed habitats in South Africa, both species are also extremely weedy in their native ranges. They frequently inhabit disturbed habitats, where they proliferate into extensive weedy populations. Both species are also renowned invaders beyond their native range (Rozefelds et al., 1999; de Almeida and Freitas, 2006; Lambdon, 2006; Fagúndez, 2007). We tested if the wider ecological tolerances of the weedy species *O. pes-caprae* and *O. purpurea* would enable them to be more successful under a wider range of ecological conditions (soil type and altitude) than the non-weedy *O. tomentosa*. If so, *O. pes-caprae* and *O. purpurea* were expected to thrive on both shale and sandstone soils, while *O. tomentosa* was expected to grow and reproduce best on shale only. Based on previous flowering phenology results (Dreyer et al., 2006), it was also expected that flowering would start earlier and continue for longer at the higher sites with cooler, moister climatic conditions. These results will have implications for the future weedy proliferation of these two species in both their native weedy and non-native invasive ranges.

2. Methods

The growth response of the two weedy (*O. pes-caprae* and *O. purpurea*) and one non-weedy species (*O. tomentosa*) to differences in soil type and altitude (with associated climatic differences) were tested through a series of transplant experiments in the Riviersonderend Mountains in the Western Cape Province, South Africa. The altitudinal gradient was used as a proxy for climate, as climatic conditions (including temperature and moisture availability) change with an increase in altitude. This location was selected, as it provides an excellent study environment with transplant facilities and comprehensive weather data available at different altitudes along the slope, and a road facilitating easy access to the summit of the mountain.

2.1. Study site

An experimental site was selected on the north facing slope of Jonaskop (33°58′00 S 19°30′00 E, altitude 1646 m) in the Riviersonderend Mountains, Western Cape Province, South Africa. On this mountain, Succulent Karoo vegetation dominates up to an altitude of 600 m above sea level. Above this altitude there is a transition through a Renosterveld ecotone to Mountain Fynbos. Correspondingly, there is a shift from shale derived soils to sandstone derived soils along this altitudinal gradient (Agenbag et al., 2008). Agenbag et al. (2004) viewed the change in soil type at 545–690 m above sea level, and the associated altitudinal climatic changes, as important barriers that shape the ranges of plant species. Shale derived soils are fine and nutrient-rich, and have a high water retention potential, while sandstone derived soils are coarse, nutrient poor and have a low water retention potential (Lechemere-Oertel and Cowling, 2001; Agenbag et al., 2008).

Three weather stations on Jonaskop are located along the slope at altitudes of 1303 m, 953 m and 545 m above sea level. They record air temperature, relative humidity, rainfall, soil moisture, wind speed and wind direction. In addition, three data loggers at 1196 m, 1044 m and 744 m altitudes record relative humidity, air temperature and soil moisture. Records have been taken every 30 min since February 2002, with some breaks due to logger failure. The daily 1400 h temperatures were used to calculate average monthly maximum temperatures, while the 0600 h temperatures were used to calculate average monthly minimum temperatures. Total rainfall for each month was added cumulatively. No rainfall data is available for 744 m, but it is presumably closest to the 953 m altitude.

Records obtained over a 3 year period (2002–2004) indicate an average decrease in temperature of 0.58 °C with every 100 m altitudinal rise and 56% less rainfall at the lowest site (315.4 mm) than at the highest site (719.6 mm) (Agenbag et al., 2008).

2.2. Study species

Oxalis tomentosa, *O. purpurea* and *O. pes-caprae* were selected for this study based on their weedy vs. non-weedy nature and specific vs. generalist edaphic preferences. Like all southern African *Oxalis*, these three species are bulbous perennial geophytes capable of vegetative reproduction through bulbil formation (Salter, 1944). Although all three species co-occur in the Darling region of the southwestern Cape, South Africa, only bulbs of *O. tomentosa* were collected there for this study. The bulbs of *O. purpurea* used in this study were collected from the Piekenierkloof Pass, and were used because they had been collected during a previous study and were thus readily available. Bulbs of *O. pes-caprae* were collected at Jonaskop.

O. tomentosa is naturally restricted to shale-derived soils, and has a centre of distribution in the Darling area of the southwestern Cape, and is not known to become weedy. It is a stemless to short-stemmed

(up to 2 cm tall) plant, with multifoliate leaves arranged in a basal rosette and a long rhizome leading to the bulb. It produces exendospermous seeds, and flowers from April to June (Salter, 1944).

O. purpurea is a variable species that displays considerable morphological and flower-colour variation. It has an extensive distribution range throughout the CFR on diverse substrates (Zietsman et al., 2008), and often becomes weedy in disturbed sites. *O. purpurea* is stemless plant, with trifoliate leaves arranged in a basal rosette and a short rhizome leading to the bulb. It produces endospermous seeds, and flowers from April to September (Salter, 1944; Dreyer et al., 2006).

O. pes-caprae is widespread in and native to the CFR, and often becomes weedy in disturbed sites on diverse substrates throughout the CFR. It is one of the most invasive plants in Mediterranean areas of the world, also spreading into subtropical and semi-arid regions. It has been reported as a serious weed in southern Europe, North Africa, South-Western Asia, China, Japan, Australia, New Zealand, various states in the USA and in South America (Guillerm et al., 1990; Barker et al., 2005; Lambdon, 2006). *O. pes-caprae* has a prominent, well-developed above-ground stem, with terminally clustered, trifoliate leaves and a long rhizome leading to the bulb. It produces endospermous seeds, and flowers from June to October (Salter, 1944; Dreyer et al., 2006).

2.3. Experimental design

Bulbs of the three *Oxalis* species were planted in containers at four different altitudes on Jonaskop. The two highest sites were in Sandstone Fynbos vegetation at altitudes of 1303 m (highest site, 1) and 953 m (middle site, 2). The third site occurs in the ecotone at 744 m (ecotonal site, 3), while the lowest site occurs at 545 m (Karoo site, 4) in Succulent Karoo vegetation (Agenbag et al., 2008). Boxes with 14 compartments (0.6 m wide, 0.64 m long, 0.3 m deep) were prepared for an earlier experiment (Agenbag, 2006), and were re-used in this study. The containers have open bottoms, but are isolated from the soil below by a layer of gravel and plastic sheeting with drainage holes. Six compartments were randomly chosen for our experiment, 3 filled with sandstone-derived soils (taken from the 953 m site) and 3 with shale-derived soils (taken from the lower edge of the gradient). For the purposes of this experiment, soil was removed from the containers and sieved to remove any unwanted *Oxalis* bulbs (especially of the weedy *O. pes-caprae*), which had accumulated in the containers. The containers were again filled with the sieved soil, and four bulbs per study species were planted per container, each at a depth of 10 cm. *O. tomentosa* and *O. purpurea* bulbs were randomly placed, while bulbs of *O. pes-caprae* were planted in a row along the side of each container.

Sites were visited twice a month to record the following data: emergence time, plant size (height x diameter for *O. pes-caprae* and *O. tomentosa*, and only diameter for stemless *O. purpurea*), number of leaves, leaf size (diameter of largest leaf), number of buds, number of open flowers and duration of flowering.

2.4. Statistical analysis

Only the plants that had emerged during each visit were included in the statistical analysis. The data were analysed with STATISTICA software with a full-factorial repeated measures analysis of variance (ANOVA) to test the effects of soil type, altitude and growing time on growth (plant size and diameter, number of leaves, leaf size) and flowering (total number of flowers and buds) separately for each of the species. Within- and between-subjects effects were tested for over time (days from the beginning of the experiment). Tukey HSD post hoc and univariate tests were used where needed to specify for variance between each treatment. LSD (least significant difference) mean separation was used in the analysis. The 0.05 p-value was used as the level for significant results. A pooled standard deviation was used to indicate 95% confidence intervals.

2.5. Time schedule

The experiment was initiated on 27 March 2007, when the soil was prepared and the *Oxalis* bulbs planted. Monitoring started three weeks later and continued approximately every second week throughout the growth and flowering season, up to the end of August. Dates of recording after the emergence of plants were: 01 May, 15 May, 30 May, 19 Jun, 03 Jul, 01 Aug, 17 Aug and 03 Sep.

3. Results

3.1. Emergence and growth

Weather changes in May entailing a temperature drop of up to 5 °C, coupled with heavy rains, triggered the onset of emergence of all three species (Figs. 1, 2). With the exception of the lowest altitude site, this weather change at least doubled the total monthly rainfall received prior to then (Fig. 1).

3.1.1. O. pes-caprae

The overall emergence of *O. pes-caprae* was high, with 80–100% of plants emerging at each of the altitudinal sites. Plants emerged faster in shale, except at the highest altitude (Fig. 2). The first sign of leaf yellowing (interpreted as stress in this study) was observed in sandstone at the lowest altitude in the middle of June. Similar stress signs were only observed later at the other altitudes (Fig. 3).

Both soil type ($p = 0.033$) and altitude ($p < 0.001$) had significant effects on *O. pes-caprae* plant size. Plants present on shale at the lowest altitudes grew significantly larger than plants on other substrates and altitudes (Tukey's test, $p < 0.05$, Fig. 4). Although the means (Fig. 4) suggest that plants grown on sandstone at the lowest altitude also had larger sizes, this is not statistically significant at the 0.05-level.

There were no significant differences in leaf size between treatments (Fig. 5). In contrast, the number of leaves differed significantly between both soil type ($p = 0.003$) and altitude ($p = 0.051$; Fig. 6). Leaf number was only statistically different (Tukey's test, $p < 0.05$) to the rest for plants grown on shale at the lowest altitude. This is clearly visible in August (Fig. 6), when it had a larger number of leaves than any of the treatments on sandstone. These marked differences in numbers of leaves decreased towards the beginning of September. The mean values (Fig. 6) show that there were more leaves on shale treatments over all altitudes.

3.1.2. O. purpurea

O. purpurea had a distinct pattern of emergence between the soil types. Nearly all individuals emerged in shale, while only 75% emerged in sandstone at the highest altitude (1303 m) and only 40% (across all sandstone sites) had emerged by day 84 (end of June) when there was already 90–100% emergence at all shale sites (Fig. 2). The first signs of leaf yellowing (stress) were observed on shale at the middle altitudes (744 m and 953 m) in June (Fig. 3), but further stress observations only became evident almost a month later in July.

Altitude and soil type had different effects on *O. purpurea* plant size at different time points (repeated measures ANOVA, $p < 0.05$). In general altitude had a strong effect on the plant size of *O. purpurea* ($p = 0.001$), while soil type did not. There was a significant interaction between these two ($p = 0.027$). Mean values in Fig. 4 show that plants on sandstone at the highest altitude remained smaller towards the end of the season. At the two highest altitudes the mean plant size on shale was also slightly smaller during the latter half of the season (Fig. 4), but these differences were not statistically significant at the 0.05-level (Tukey's test and univariate).

Neither soil type nor altitude had an effect on the leaf size in *O. purpurea* (Repeated measures ANOVA, $p > 0.05$, Fig. 5). Overall only altitude had an effect ($p = 0.037$) on the number of leaves, but this effect differed at different time points. At the beginning of the season

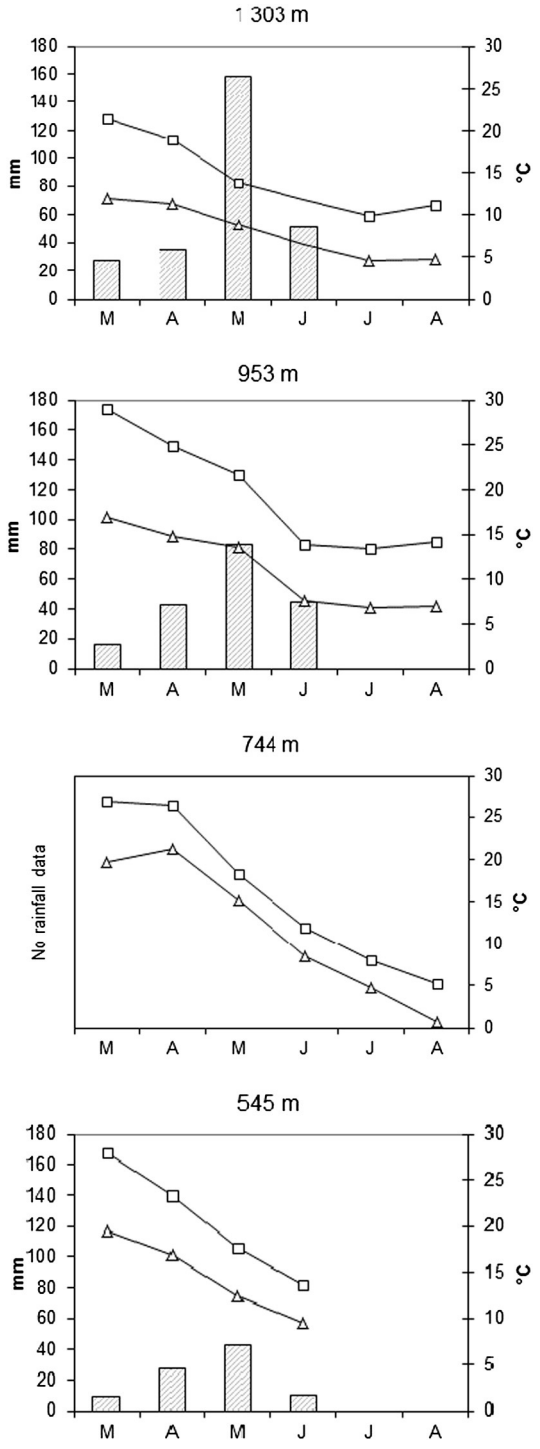

Fig. 1. Weather data along the altitudinal gradient. Monthly total rainfalls are in columns and maximum (□) and minimum (Δ) temperatures as lines. There is no rainfall data available for 744 m, but it is assumed to be close to that of 953 m. Due to equipment failure temperature data are missing at 545 m from 16/06 onwards, at 953 m no data were logged from 20/05 to 15/06 and at 1303 m temperature data are missing between 15/06 and 30/06. No rainfall data was logged after June.

soil may also have had a slight effect on leaf numbers, as plants grown on sandstone at the highest altitude had the fewest leaves (Tukey's test, $p < 0.05$, Fig. 6).

3.1.3. O. tomentosa

O. tomentosa emergence showed no preference for soil type, unlike the emergence of the other two species, but a clear altitude-effect was detected. Emergence at the highest altitude was slower and in total never exceeded 70%, while emergence at lower altitudes was 80–100% by the beginning of June (Fig. 2).

Altitude and soil type had no significant effect on *O. tomentosa* plant size during any time point (Fig. 4), but altitude had a near significant effect ($p = 0.082$) on leaf size (Fig. 5). Soil type affected the number of *O. tomentosa* leaves that developed, but the effect differed over time. On sandstone the number of leaves was still increasing at the end of the experiment (Tukey's test and univariate, $p < 0.05$, Fig. 6). Altitude also affected the number of leaves ($p = 0.014$), but only towards the end of the season for some of the treatments (Tukey's test, $p < 0.05$).

In general *O. tomentosa* was not successful under any conditions, and did not flower in any soil type or at any altitude.

3.2. Flowering phenology

3.2.1. O. pes-caprae

In *O. pes-caprae* flowering (buds) was initiated first at the lowest altitude (545 m) by the last days of May (Figs. 3, 7). This was identical on both soil types. This lowest altitude site received 27–50% less rain during May and was on average 4–9 °C warmer than the highest site (Fig. 1). At the highest altitude (1303 m) flowering only started about two months later in August (Fig. 3). Flowering was delayed by increasing altitude, moister and cooler conditions. At all altitudes flowering was also less abundant in sandstone than in shale (Fig. 7). However, at the lowest site, *O. pes-caprae* finally produced almost the same number of flowers on both soil types towards the end of the season. By far the highest reproductive output in shale was achieved at the two lowest altitudes. Although data collection was suspended after the beginning of September (Fig. 3), *O. pes-caprae* still flowered at the end of September at all sites, and at the beginning of October there were still some flowers at the highest altitude on shale, when flowering had finished at all other sites.

Results for the number of flowers produced per plant were similar to results for plant size in *O. pes-caprae*. Both soil type and altitude had an effect on the number of flowers per plant (Repeated measures ANOVA, $p = 0.003$). These differences were seen towards the end of the season: plants had significantly more flowers at the last two time points on shale and at the two lowest altitudes (545 m and 744 m) (Tukey's test, $p < 0.05$, Fig. 7).

Overall *O. pes-caprae* grew bigger and produced more flowers on shale, at the lowest altitudes, and under the warmest and driest conditions tested.

3.2.2. O. purpurea

O. purpurea generally produced much fewer flowers than *O. pes-caprae* (Fig. 7). Unlike in *O. pes-caprae*, the effects of soil type and altitude on flower numbers were unclear in *O. purpurea*. Plants grown in sandstone at the middle altitudes sites (744 m and 953 m) produced the most flowers, while plants at the highest altitude (1 303 m) produced fewer flowers. Sandstone soils yielded more variation in numbers of buds and flowers over time, while flowers and buds increased more steadily on shale soils (Fig. 7). The longest flowering period was observed on both substrates at the middle site (953 m), which was exposed to fairly average climatic conditions (Figs. 1, 3).

There were fewer flowers on sandstone than on shale towards the end of the season starting from 1 August at the highest altitude (Tukey's test and univariate, $p < 0.05$). The mean values also displayed this pattern at other time points, but without statistical significance (Figs. 3 and 7). The observed significant results towards the end of the season explain the 3-way interaction of altitude, soil and time ($p < 0.05$).

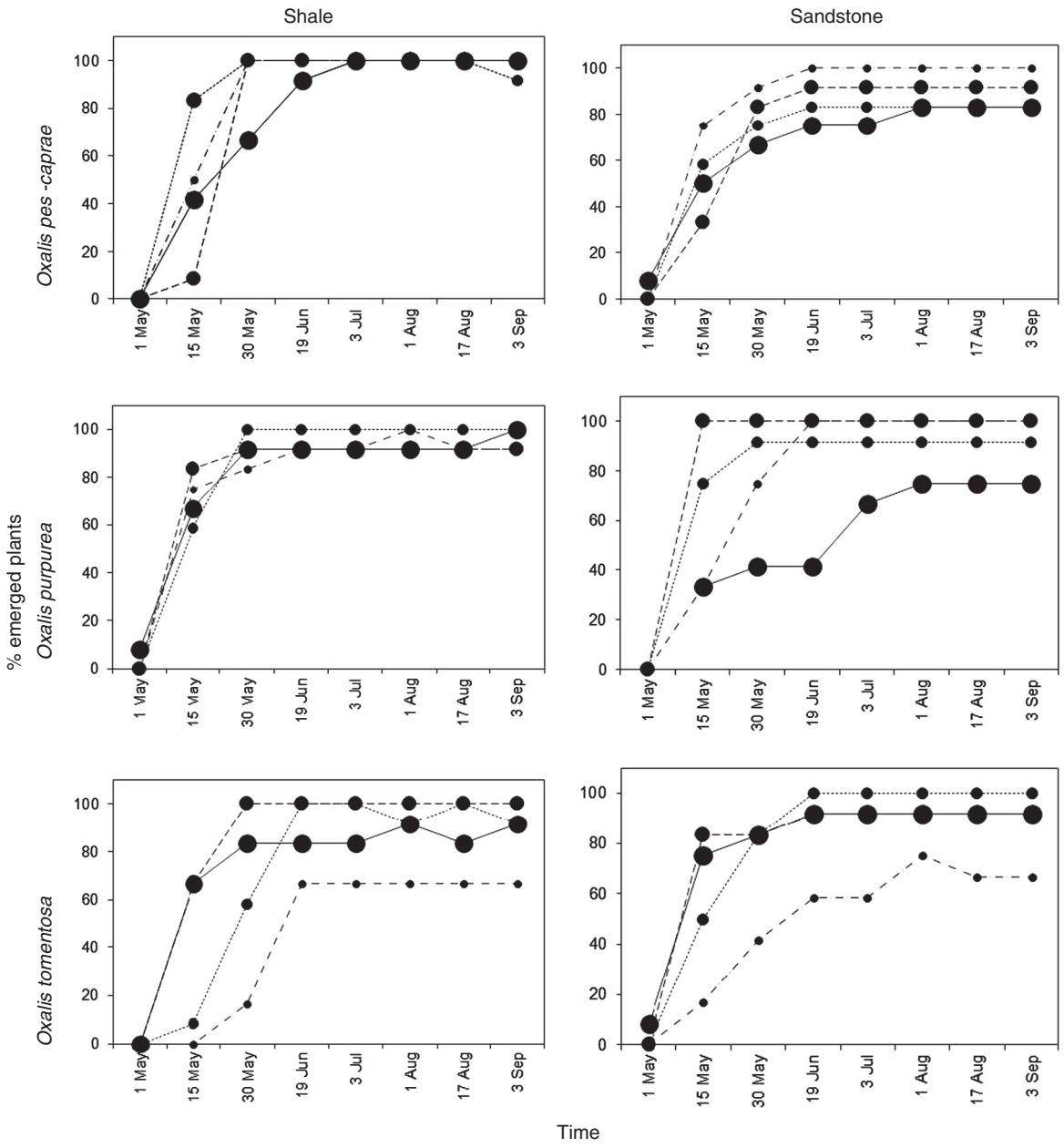

Fig. 2. Percentage of emerged plants over time for *Oxalis pes-caprae*, *O. purpurea* and *O. tomentosa*. Altitudes are displayed as round shapes of increasing size with increasing altitude so that the largest circle represents 1303 m, second largest 953 m, third largest 744 m and smallest 545 m above sea level.

In general *O. purpurea* grew and flowered similarly under all conditions. Only on sandstone at the highest site did growth slow down towards the end of the time period.

4. Discussion

To limit plant invasion and its potential ecological impacts, it is crucial to identify the underlying causes of invasiveness. The success of invasive species has been ascribed to a diversity of traits (Rejmánek and Richardson, 1996; Goodwin et al., 1999; Widrlechner et al., 2004; Rejmánek et al., 2005a), especially in disturbed habitats (Hannah et al., 1994). Important life history traits include fast relative growth rate (Grotkopp et al., 2002; Burns, 2004, 2006), and reproductive traits such as short generation time, small seeds, short intervals between large seed crops, high seedling relative growth rate, the attractiveness of fruits and long fruiting periods (Reichard, 1994; Rejmánek and Richardson, 1996; Widrlechner et al., 2004; Grotkopp and Rejmánek, 2007). If the new environment is not readily invasible, introduced species should display sufficient phenotypic plasticity to maintain fitness in the new environment and/or undergo rapid adaptation (Hulme and Barrett, 2013; Pyšek and Richardson, 2012). Kolar and Lodge (2001) identified the ability to reproduce vegetatively as the most important trait in invasive plants. Te Beest et al. (2011) reviewed the role of polyploidy in facilitating plant invasions, and found polyploids to be predisposed to have higher survival rates, increased growth and phenotypic plasticity, enabling plants to overcome the environmental barriers of invasion. Polyploidy causes increased plant, flower and seed sizes, and attributes such as a prolonged flowering period and/or large plant size help facilitate establishment in new habitats. The physiology of polyploids allows for higher hormone concentrations, drought and stress tolerance and increased transpiration rate and photosynthetic activity (Te Beest et al., 2011).

Rejmánek et al. (2005b) argued that areas with Mediterranean climates are more vulnerable to plant invasions, while Godoy et al.

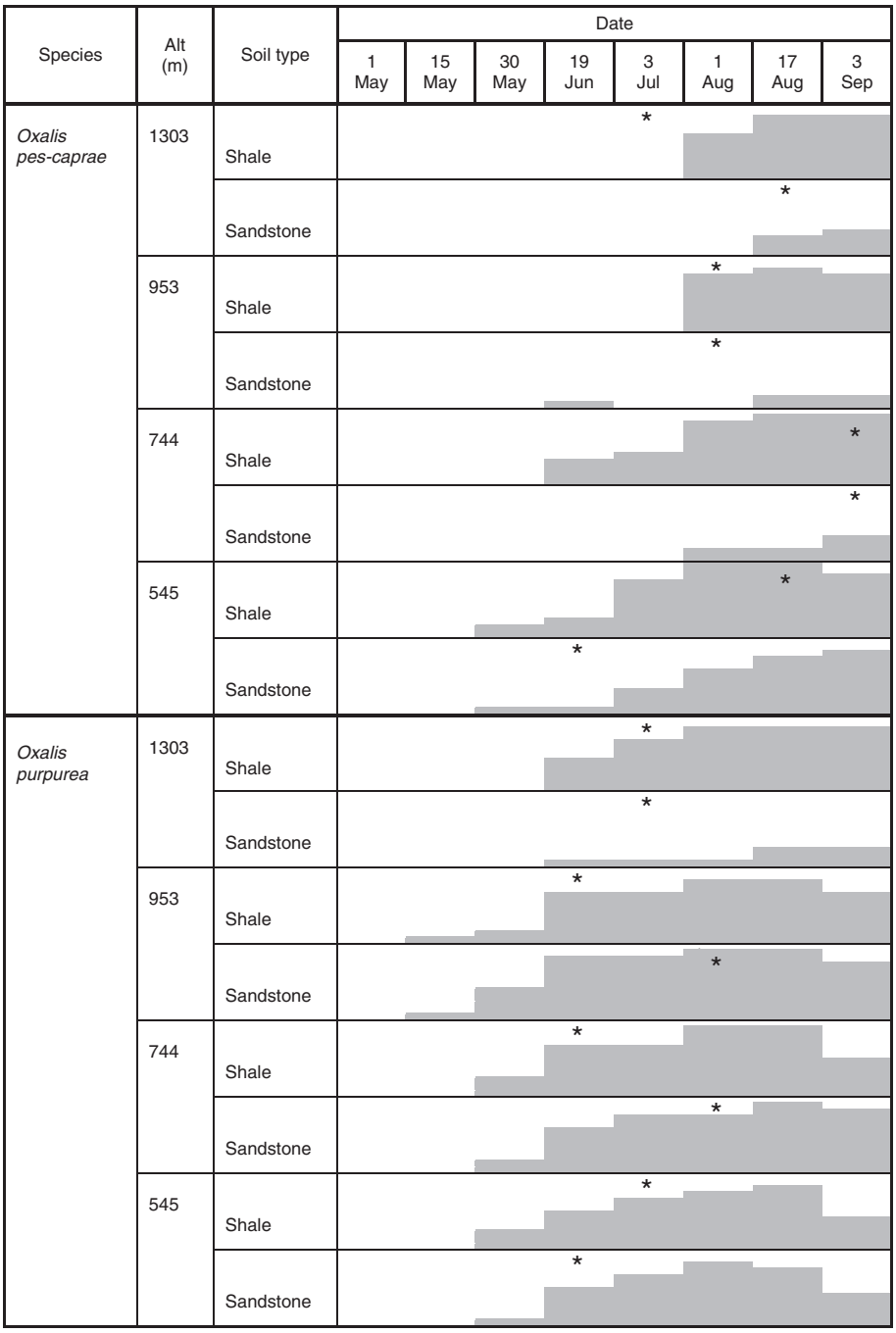

Fig. 3. Timing of budding and flowering in *Oxalis pes-caprae* and *O. purpurea*, arranged by altitude and soil type. Time is in days from planting of bulbs. Height of shaded bars indicates the number of plants out of 12 in bud or flower. The first signs of stress (leaf yellowing) at each altitude are marked with *.

(2009) found invasive plants in the CFR to flower for longer than CFR natives. *O. pes-caprae* is known as a serious international weed in especially Mediterranean climate regions of the world (Lambdon, 2006). It has also become extensively weedy within its native range. This species is known to display high levels of polyploidy in both its native (Krejčíková et al., 2012) and invaded ranges (Castro et al., 2007). It is able to effectively colonize disturbed sites (Ghebremariam, 2004), mainly through its profuse ability to reproduce vegetatively through bulbil formation (Pütz, 1994). In the Mediterranean region *O. pes-caprae* has been shown to negatively impact the original vegetation. Petsikos et al. (2007) found that intensive *O. pes-caprae* invasion reduced the numbers of species present in olive groves in Greece by up to 75%. *O. pes-caprae* also reduced the net primary productivity of the system, such that its invasion had considerable effects on the original vegetation. *O. purpurea* has also become extensively weedy within its native range (Salter, 1944), and is known to have invaded Australia, Tasmania and Mediterranean regions in Europe (Rozefelds et al., 1999; de Almeida and Freitas, 2006; Fagúndez, 2007). *O. purpurea* invasions are, however, much less extensive than those of *O. pes-caprae*. It is also known to display considerable levels of polyploidy in its native range (Dreyer, unpublished data).

The potential impact of future invasions of *O. pes-caprae* or *O. purpurea* on native fynbos vegetation under predicted models of future climate change has not yet been tested. Fynbos species are drought-sensitive and dependent on reliable and substantial winter rainfall. Reduced rainfall figures, as have been predicted by climatic models (Midgley et al., 2005), would cause such fynbos species to experience stress, and would thus render such fynbos communities more vulnerable to invasion. It has been projected that depending on the

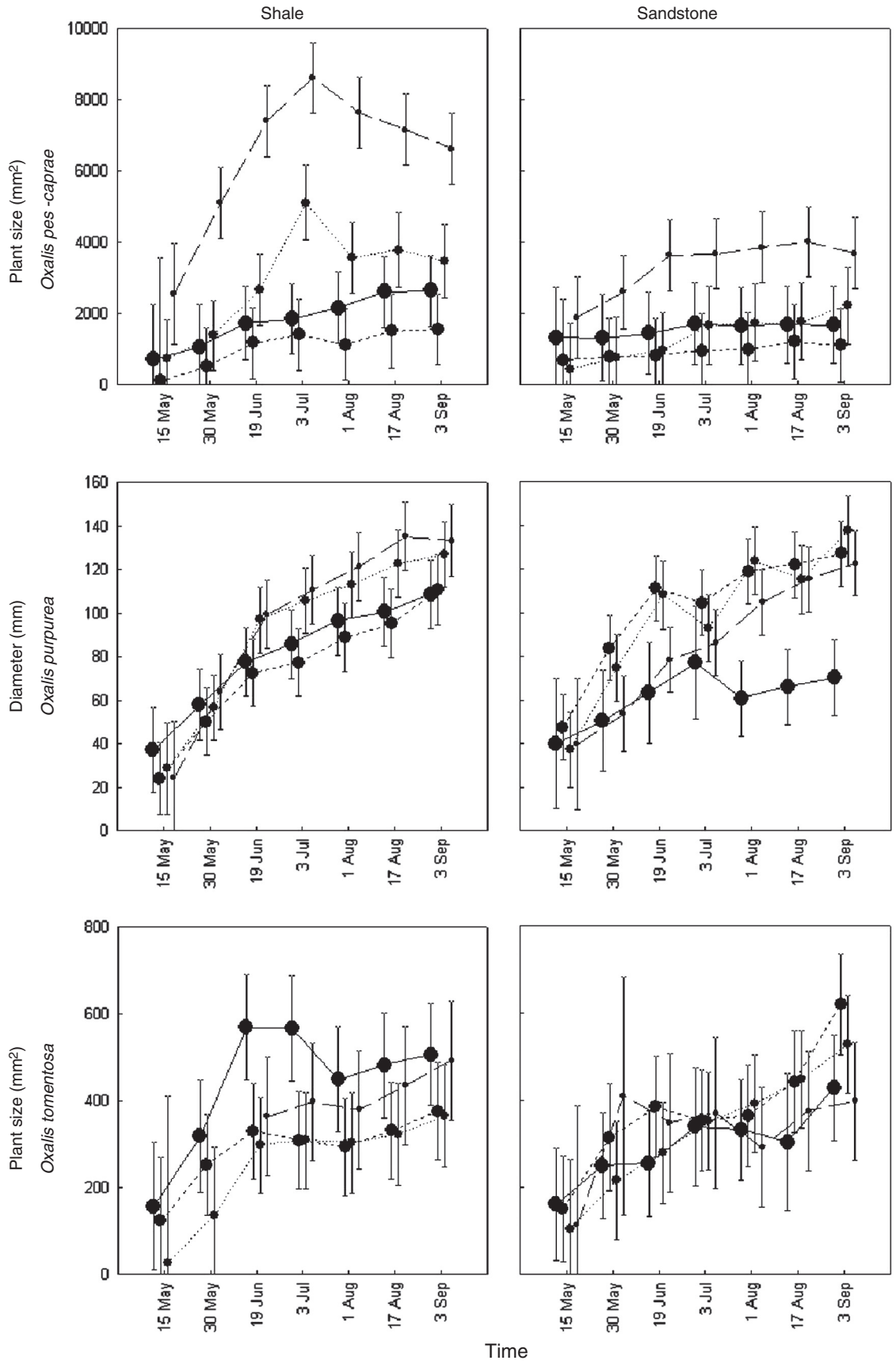

Fig. 4. Plant size measured as height × diameter (mm^2) for *Oxalis pes-caprae* and *O. tomentosa*, and only diameter (mm) for *O. purpurea*, over time at the different altitudes. Note the difference in scale of the horizontal axis. Vertical bars show 95% confidence intervals. Altitudes are displayed as round shapes of increasing size with increasing altitude so that the largest circle represents 1303 m, second largest 953 m, third largest 744 m and smallest 545 m above sea level.

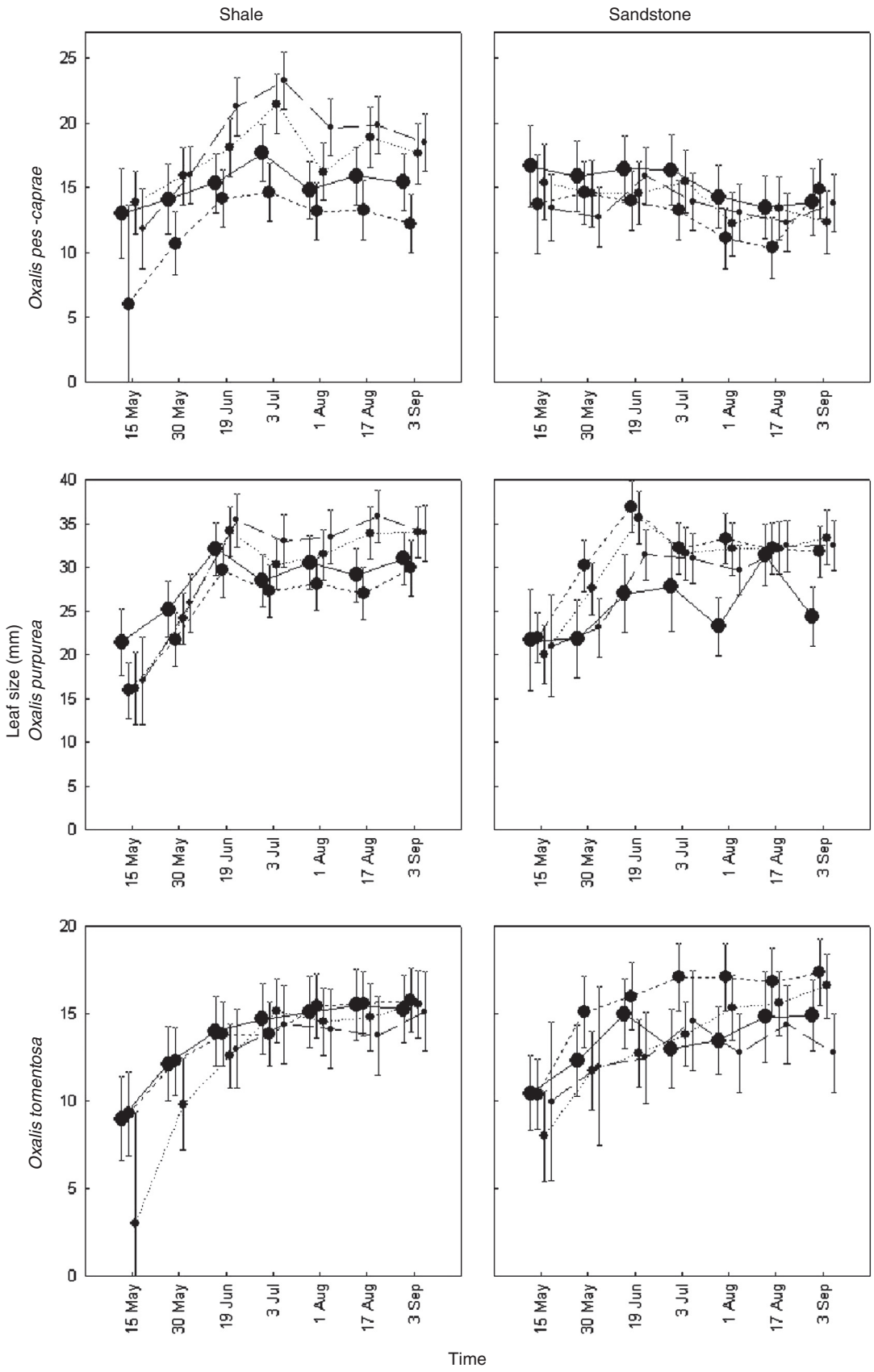

Fig. 5. Leaf size (mm) of *Oxalis pes-caprae*, *O. purpurea* and *O. tomentosa* over time at the different altitudes. Vertical bars show 95% confidence intervals. Note the difference in scale of the horizontal axis. Altitudes are displayed as round shapes of increasing size with increasing altitude so that the largest circle represents 1303 m, second largest 953 m, third largest 744 m and smallest 545 m above sea level.

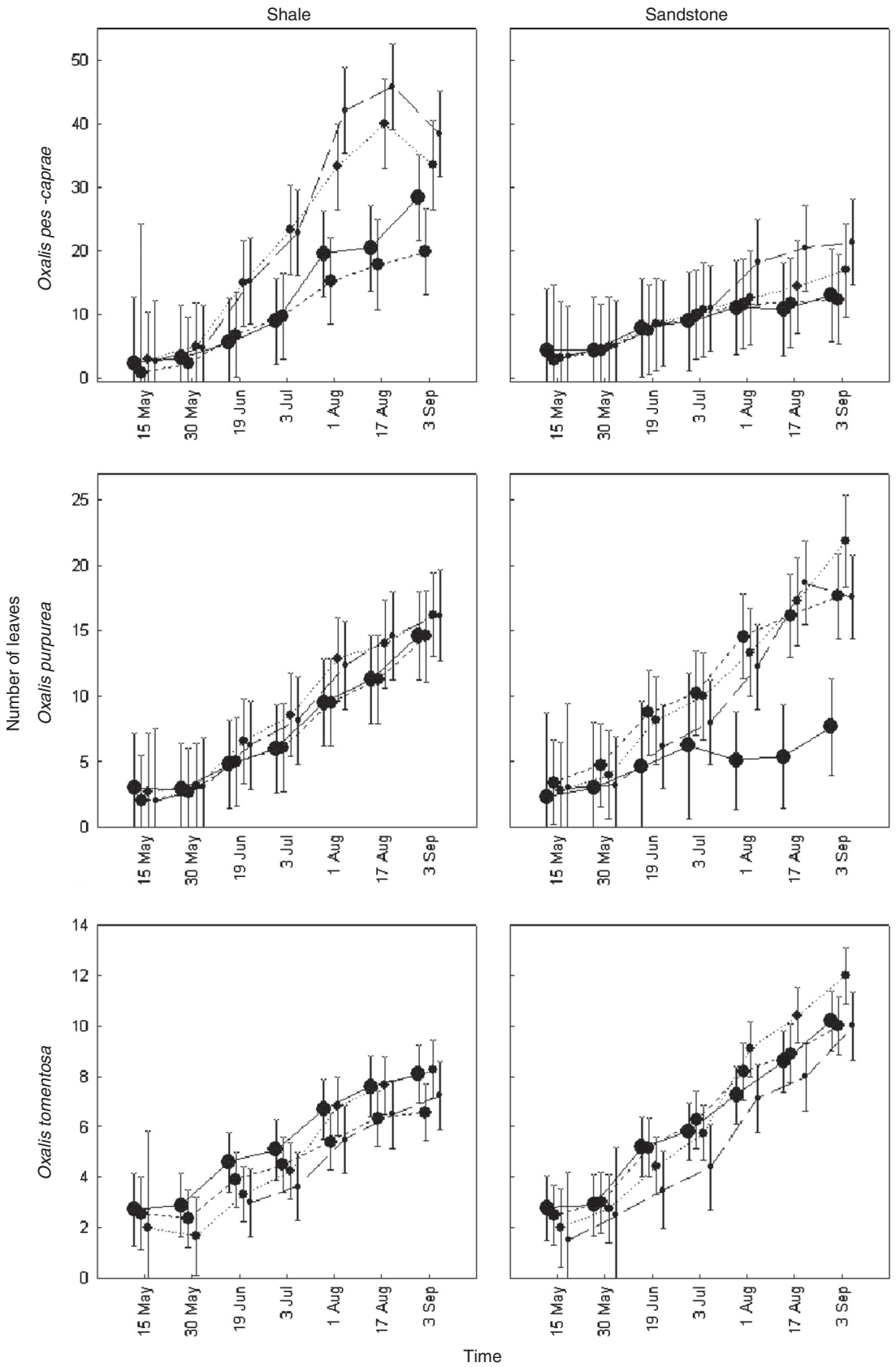

Fig. 6. Number of leaves on *Oxalis pes-caprae*, *O. purpurea* and *O. tomentosa* over time (days) at the different altitudes. Vertical bars show 95% confidence intervals. Note the difference in scale of the horizontal axis. Altitudes are displayed as round shapes of increasing size with increasing altitude so that the largest circle represents 1303 m, second largest 953 m, third largest 744 m and smallest 545 m above sea level.

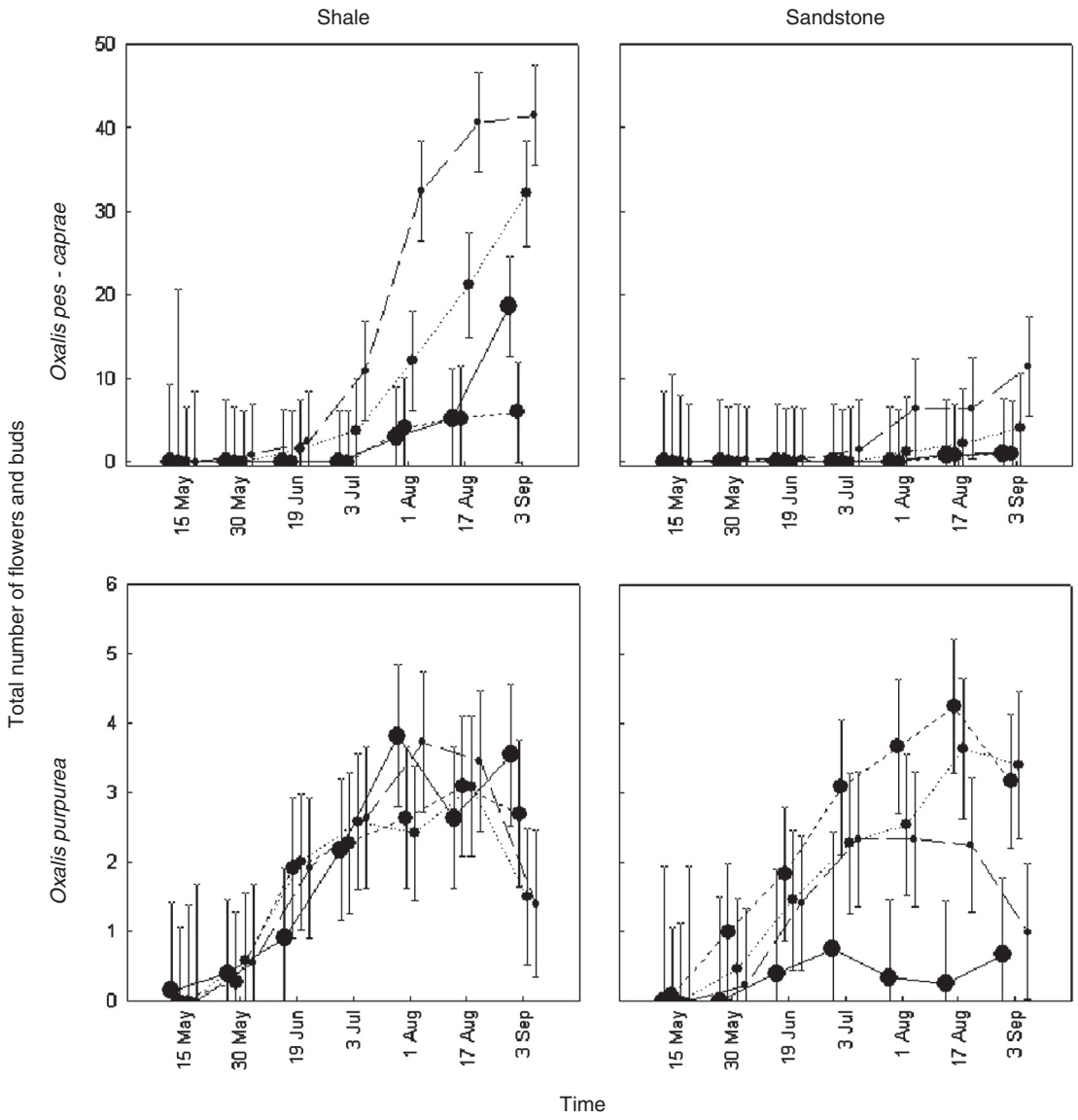

Fig. 7. Total number of flowers and buds for *Oxalis pes-caprae* and *O. purpurea*. Vertical bars show 95% confidence intervals. Note the difference in scale of the horizontal axis. Altitudes are displayed as round shapes of increasing size with increasing altitude so that the largest circle represents 1303 m, second largest 953 m, third largest 744 m and smallest 545 m above sea level.

climate change model Cape Fynbos would lose 51–65% of its area by 2050 (Midgley et al., 2002). Disturbance imposed on the original plant community, caused by climate may enable weedy *Oxalis* to invade new areas. The restrictions imposed by substrate, however, should hinder some *Oxalis* species from invading higher altitudes to a threatening extent.

Our results indicated the increased weedy and/or invasive traits of some of the studied species above others. The three species showed different responses to environmental conditions. *O. pes-caprae*, identified as the weediest species, showed the best adaptability to warmer and drier conditions, as growth and flowering increased at lower altitudes. This should enable *O. pes-caprae* to invade higher altitudes if the region is to experience warmer and drier climatic conditions in future. Such an invasion may, however, be curtailed by substrate, as *O. pes-caprae* showed reduced growth and reproductive success on sandstone. Like Jonaskop, most Cape Mountains comprise of fynbos-inhabited sandstone derived soils at altitudes above 500 m (Linder, 2003). *O. purpurea*, in contrast, was only restricted by soil type at the highest altitude, suggesting that this species has a wider environmental tolerance. It also had the longest flowering period at high altitudes and on sandstone. It is thus better adapted to a wide range of current climatic conditions, but would not profit from predicted future warmer and drier conditions. *O. tomentosa*, as a habitat-specific species, was stressed at all sites and did not show differences in growth under any conditions. The expected preference to the shale substrate did not emerge as its growth success (or indeed lack thereof) was similar on both substrates. The most likely explanation for this is that *O. tomentosa* is a lowland species, naturally occurring only at altitudes of between 75 and 150 m (Dreyer and Makgakga, 2003), which is substantially lower than even the lowest altitude at the study site. It thus appears as if *O. tomentosa* is highly restricted by altitude, rendering it an unlikely candidate ever to become aggressively invasive.

Results of the flowering phenology of the species studied correspond to results obtained by Dreyer et al. (2006), who suggested that flowering in *Oxalis* is initiated by the onset of winter rains combined with a drop in temperatures. They also showed that warmer and drier

conditions shortened the flowering period of the *Oxalis* species they studied. Our results contradicted this, however, as *O. pes-caprae* flowered for longer in drier and warmer sites. *O. purpurea* experienced a slightly longer flowering period under cooler and moister conditions.

Our results show that soil and climate are important determinants in the success of *Oxalis*-species: these environmental conditions influence the success of individual species. Changes to climatic conditions may therefore have an impact on the future vegetation composition in the CFR. Weedy species such as *O. pes-caprae* are expected to be the ones that will profit most from the projected disturbances.

Acknowledgments

The Du Plessis family and SENTECH are acknowledged for allowing access to the study site and helpful ongoing support. This study was financially supported through an NRF grant (Gun: 2053585) to L.L. Dreyer and the Centre for Invasion Biology (to K.J. Esler). We acknowledge the support from SANBI and especially field assistance provided by Deryck de Wit. CapeNature is acknowledged for issuing the necessary collection permits. Comments from anonymous reviewers helped to improve the manuscript.

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